

When Is Self-Organization Used in Biological Systems?

THOMAS D. SEELEY

Department of Neurobiology and Behavior, Mudd Hall, Cornell University, Ithaca, NY 14853

Abstract. Self-organization, or decentralized control, is widespread in biological systems, including cells, organisms, and groups. It is not, however, the universal means of organization. I argue that a biological system will be self-organized when it possesses a large number of subunits, and these subunits lack either the communicational abilities or the computational abilities, or both, that are needed to implement centralized control. Such control requires a well informed and highly intelligent supervisor. I stress that the subunits in a self-organized system do not necessarily have low cognitive abilities. A lack of preadaptations for evolving a system-wide communication network can prevent the evolution of centralized control. Hence, sometimes even systems whose subunits possess high cognitive abilities will be self-organized.

Introduction

Self-organization is widespread in biological systems. That is to say, it is common to find biological systems that function without guidance from an external controller, or even from an internal control center. Instead, we often find that biological systems function with mechanisms of decentralized control in which the numerous subunits of the system—the molecules of a cell, the cells of an organism, or the organisms of a group—adjust their activities by themselves on the basis of limited, local information. An apple tree, for example, “wisely” allocates its resources among woody growth, leaves, and fruits without a central manager

of its cells. Likewise, an ant colony “intelligently” distributes its work force among such needs as brood rearing, colony defense, and nest construction without an omniscient overseer of its workers. Much of the challenge in understanding the inner workings of living systems arises from their use of decentralized control mechanisms, which are harder for the human mind to grasp than centralized control mechanisms. This is why mathematical models, computer simulations, and the other tools used by investigators of self-organization (Bonabeau *et al.*, 1997; Camazine *et al.*, 2001) are helpful in building a solid understanding of how living things work.

Given that self-organization is widespread in biological systems, the question arises of why this is the case. In this essay, I will share my thoughts on this issue. My views derive partly from what I have learned through studying one of nature’s most accessible self-organized systems, the honeybee colony, and partly from what I have learned through reading various works in the fields of biology, economics, and engineering.

The biological systems I will be considering are all ones in which the genetics interests of the system’s subunits are largely, if not entirely, congruent; hence the subunits cooperate closely for the effective functioning of the system as a whole. Such systems are what Dawkins (1982) has called *vehicles*: thoroughly integrated entities that have evolved to foster the survival and reproduction of the genes they contain. These systems include single-celled creatures, multicellular organisms, and even some animal societies, such as colonies of honeybees and army ants. Hence, this essay relates to the general issue in biology of how functionally integrated entities arise, or individuation occurs, at various hierarchical levels (Maynard Smith and Szathmáry, 1995; Seeley, 1995; Bonner, 1998; Sober and Wilson, 1998; Keller, 1999; Michod, 1999; Wilson, 1999). In addressing the question of where self-organization occurs in biological

E-mail: tds5@cornell.edu

This paper was originally presented at a workshop titled *The Limits to Self-Organization in Biological Systems*. The workshop, which was held at the J. Erik Jonsson Center of the National Academy of Sciences, Woods Hole, Massachusetts, from 11–13 May 2001, was sponsored by the Center for Advanced Studies in the Space Life Sciences at the Marine Biological Laboratory, and funded by the National Aeronautics and Space Administration under Cooperative Agreement NCC 2–896.

systems, we examine an issue that applies across the hierarchical spectrum.

The Importance of Communicational and Computational Abilities

My basic argument is this: a biological system will be self-organized if it consists of a large number of subunits, and these subunits do not possess the communicational and computational abilities needed to implement centralized control, which necessarily involves a well informed and highly intelligent supervisor.

As Friedrich von Hayek (1945) and Herbert Simon (1962) pointed out long ago, centralized control of any large system requires (1) that a tremendous amount of information—usually dispersed among all the subunits of the system—be communicated to a central decision-making body (one subunit or a group of subunits), (2) that this body integrate all this information to decide a course of action, and (3) that it then issue instructions to the other subunits in the system. When we look across the range of functionally integrated entities in nature, we see that some have indeed evolved the sophisticated communicational and computational mechanisms required for some degree of centralized control. In the adult form of many metazoan organisms, for example, we find an elaborate peripheral nervous system that makes possible the rapid transmission of information throughout the organism, and a sophisticated central nervous system that processes the sensory input and decides most of the motor output for the organism. Likewise, in some of the colonial marine invertebrates, particularly the swimming colonies of the Siphonophora, we find a colony-wide network of nerves and a simple brain that together support a rudimentary level of centralized control of the propulsion zooids within a colony (Mackie, 1986). And, obviously, we humans have developed sophisticated communicational and computational technologies that make it possible for certain human groups, notably military and manufacturing units, to function with a high level of centralized, hierarchical control (Bartholdi, 1993).

Besides these biological systems that function with some degree of centralized control, there are many others that operate with little or no central authority. These are self-organizing systems. Their subunits have not evolved either broad communicational networks or powerful computational abilities; thus it is not surprising that they operate without central planning. For instance, no species of social insect has evolved anything like a colony-wide communicational network that would enable information to flow rapidly and efficiently to and from a central manager. Moreover, no individual within a social insect colony is capable of processing huge amounts of information. (Contrary to popular belief, the queen of a colony is not an omniscient individual that issues orders; rather, she is an oversized

individual that lays eggs. The biblical King Solomon was correct when he noted, in reference to ant colonies, there is “no guide, overseer, or ruler” [Proverbs 6:7]). Therefore, it is not surprising that social insects with large colonies provide us with striking examples of self-organized systems. Other good examples in biology are multicellular animals during development—that is, before they have assembled their communicational networks (peripheral nervous systems) and central computers (central nervous systems); plants at all levels of evolutionary sophistication (nonvascular and vascular forms); and bacterial colonies (reviewed in Camazine *et al.*, 2001; see also Shapiro and Dworkin, 1998).

Why Is There Self-Organization?

Given that some biological systems have evolved centralized control, it is clear that self-organization is not always the best means of coordinating the subunits in a system. The absence of a central authority leaves a system (of molecules, of cells, or of organisms) prone to opposing actions among its subunits, for they will respond to their different, local conditions rather than to the shared, global situation of the system as a whole. Colonies of social insects frequently experience this problem, such as when an ant colony changes nest sites and some workers carry brood items out of the old site while others carry them back in again (Wilson, 1971, p. 224). Also, when no one is supervising a system, needless redundancies are apt to arise within it. The IBM corporation experienced precisely this problem in the 1980s when it decentralized its operations and costly duplications of activities arose among its divisions (Drucker, 1988). Furthermore, the absence of a centralized authority within a system can limit its ability to find the globally optimal solution to a problem and can even render it vulnerable to getting stuck in a pathological state. A gruesome example of this is the “circular mill” of *Eciton* army ants in Guyana that William Beebe (1921; cited in Anderson and Bartholdi, 2000) described: a circle, measuring some 100 m in diameter and lasting for two days, of ants continuously following each other round and round, and gradually dying from exhaustion. In short, systems with decentralized control can easily lack “the vision thing.”

Despite the potential problems of decentralized control (self-organization), many biological systems do rely on it. One can ask whether these systems have been unable to evolve mechanisms of communication and computation sufficient to support centralized control (*i.e.*, centralized control is an adaptive peak, but one that is hard to reach) or whether they have experienced selection pressures that favor low communicational abilities or low computational abilities, or both (*i.e.*, centralized control is *not* an adaptive peak). I believe that the first reason explains the widespread existence of self-organization in social insect colonies. The

subunits in these colony-level systems, unlike those in organism-level and cell-level systems, do not form stable, physical connections. With the exception of human groups, which possess advanced technologies for communication, all biological systems with powerful communication networks have their subunits arranged in stable configurations with solid connections between the subunits. Such spatial stability and connectivity evidently facilitates the evolution of a system-wide communication network. Thus it appears that colonies of social insects, whose workers typically move about within the nest, lack a crucial preadaptation for evolving sophisticated, colony-wide communication systems.

The second possible reason for decentralized control, that it is more adaptive than centralized control, may apply in situations where the high costs of centralized control are not compensated by high benefits. Certainly there are high costs to having the sophisticated communicational and computational abilities that underlie centralized control. Just consider the high metabolic costs of maintaining the nervous system of a metazoan organism, or the high financial costs of maintaining the industrial engineering department of a manufacturing enterprise. One American food distributor, for example, employs two engineers and one programmer to maintain the work-content models for managing their warehouses, at a cost of \$250,000 annually (B. Little, Manhattan Associates, cited in Anderson and Bartholdi, 2000). For centralized control to evolve, such high costs must be outweighed by high benefits. It is not hard to imagine situations where there are actually *low benefits* to having centralized control. One is when a biological system is highly susceptible to the loss of subunits, perhaps through predation or disease. In a system with centralized control, the loss of the central manager can result in a catastrophic failure of the entire system. In contrast, systems with decentralized control are generally robust to the loss of subunits. Anderson and Bartholdi (2000) compare the characteristics of centralized and decentralized control paradigms and discuss the logistical situations in which each type of control is likely to yield high benefits. Their article focuses on manufacturing operations, but because it is inspired by the ways that social insects have solved problems of colony organization, it has much relevance to biological systems.

Self-Organization and the Cognitive Abilities of Subunits

I have presented the view that high communicational and computational abilities in a system's subunits are essential for the evolution of centralized control in large systems, for without such abilities centralized control cannot be implemented. This view implies that biological systems whose subunits lack broad communicational abilities or sophisticated computational (cognitive) abilities, or both, must

function with decentralized control. I wish to stress, however, that the subunits in a self-organized system do not necessarily have low cognitive abilities. The subunits might possess cognitive abilities that are high in an absolute sense, but low relative to what is needed to effectively supervise a large system. A human being, for example, is an intelligent subunit in the economy of a nation, but no human possesses the information-processing abilities that are needed to be a successful central planner of a nation's economy. It is also possible that the subunits possess high cognitive abilities, but are in a system that lacks an extensive communication network. Such subunits would be *highly intelligent*, but *poorly informed*. A worker honeybee, for example, is an intelligent creature (see below) that functions in a system that lacks a communication network capable of supporting centralized control.

It is important to consider the issue of the cognitive abilities of the subunits in decentralized (self-organized) systems because it points to a fundamental flaw in many studies of self-organization: the assumption that the subunits in a self-organized system are dumb. This viewpoint is generally expressed in terms of "simple individuals" (e.g., Goss and Deneubourg, 1988; Strickland *et al.*, 1993) following "very simple rules of behavior" (e.g., Camazine *et al.*, 1990; Jenkins *et al.*, 1992; Strickland *et al.*, 1992) or executing "simple stimulus-response acts" (Camazine *et al.*, 2001, p. 488). It is certainly true that many studies have shown that decentralized control can produce complexity at the system level—for example, the intricate nests and foraging operations of social insect colonies—without need for comparable complexity at the individual level (Theraulaz and Bonabeau, 1995; Bonabeau, 1998; Theraulaz *et al.*, 1998; Karsai, 1999). This does not, however, prove that the subunits in the systems studied lack behavioral complexity and high cognitive abilities; it indicates only that the subunits did not show complexity in these studies, most of which involve a deliberate simplification or even a mere simulation of reality.

The implicit assumption of dumb subunits underlying most studies of self-organization could be tested for social insects by looking at individual complexity in relation to colony size. If individual complexity decreases as colony size (and decentralization/self-organization) increases, the dumb subunits paradigm gains credence. However, there is no compelling evidence of an inverse relation between individual complexity and colony size (Anderson and McShea, 2001). The workers of large colonies do show a loss of totipotency, especially with respect to reproductive potential (Crespi and Yanega, 1995; Bourke, 1999), and they do show a loss of structures associated with reproduction (e.g., ovaries in ants); but they do not show signs of reduced behavioral or cognitive complexity. Indeed, one can make a strong argument that the cognitive complexity of individuals needs to be greater in species with large colonies than in

those with small colonies, especially when the workers do not have lifelong task specializations (e.g., physical polyethism) but instead perform different tasks at different stages of life (e.g., temporal polyethism). As colony size evolves to higher levels, new ecological opportunities and problems arise that can favor the evolution of additional behaviors, such as recruiting to food sources, activities for fighting diseases, colonial thermoregulation measures, and coordinated ambushing of prey. Also, new, more efficient ways of organizing work can evolve, such as task partitioning (Jeanne, 1986; reviewed by Ratnieks and Anderson, 1999) and teamwork (Anderson and Franks, 2001); and these necessitate the evolution of behavioral mechanisms for coordinating the individuals working together on a task. Bonner (1988) makes similar arguments for systems of cells in the evolution of multicellular organisms: as the size of an assemblage of cells increases, new opportunities and new needs arise for more sophisticated methods of food acquisition, gas exchange, and internal circulation.

My view that self-organized systems can be composed of subunits possessing high cognitive abilities is based on my experience in analyzing the functional organization of honeybee colonies. These are large biological systems that function with decentralized control (Seeley, 1995) and that are composed of subunits—worker bees—whose cognitive sophistication is certainly impressive. One indication of this sophistication is the large number of signals (17) and cues (34) that we know workers are sensitive to inside a hive (reviewed in Seeley, 1998). Another indication is the remarkable behavioral versatility of worker bees and their impressive ability to integrate information when deciding how to behave: they do not follow “very simple rules of behavior” or execute “simple stimulus-response acts.” Consider, for example, the actions of a worker bee scouting a nest site, starting when she has discovered a promising tree cavity. She first spends 20–40 minutes inspecting the site, acquiring information about the cavity’s volume, the size of its entrance, its height off the ground, its exposure to sun and wind, and still other variables (Seeley, 1977; Seeley and Morse, 1978). In short, she makes a multifactorial evaluation of her find. She then integrates the information that she has acquired about her site to determine its overall desirability as a future dwelling place. Next, she returns to the swarm cluster, where she performs a waggle dance to advertise her site to the other scout bees (Lindauer, 1955). Because the recruitment target is small, just the entrance opening to her site, she adopts a special form of the dance; she produces waggle runs with less directional scatter (thereby indicating the target’s direction with greater precision) than she would if she were advertising a spacious patch of flowers (Weidenmüller and Seeley, 1999). Moreover, she skillfully adjusts both the duration and the rate of her production of waggle runs in relation to the desirability of her site (Seeley and Buhrman, 2001), and she gradually

reduces the number of waggle runs produced per return to the swarm over sequential returns (Seeley, unpubl.). All of these tunings of her dance behavior are important to the consensus-building process whereby the scouts of a swarm collectively choose its new home. Once the swarm’s domicile has been chosen, our scout somehow senses this, ceases waggle dancing, and starts producing a different signal, called *wings-together piping*. This signal stimulates the non-scouts in the swarm to warm themselves to a flight-ready temperature (35°C) in preparation for liftoff (Seeley and Tautz, 2001). Finally, once all the bees in the swarm are suitably warmed, the scout stops piping and starts producing a third signal, called *buzz running*, which triggers the break-up of the cluster (Lindauer, 1955; Esch, 1967).

There can be no doubt that a worker honeybee is a sophisticated piece of biological machinery; one that is exquisitely sensitive to its environment and that makes intricate adjustments of its behavior in adaptation to the ever-changing state of its environment. After all, the sketch just painted of a scout bee’s actions does not capture the full complexity of her behavior, and the complexity of a scout bee’s behavior is but a small fraction of the full complexity of a worker bee’s behavior across her life (when she also functions as a cleaner bee, nurse bee, food-storer bee, forager bee, etc.). Such complexity in the behavior of a worker bee shows us that the subunits in a self-organized system can possess a high level of cognitive sophistication. This fact must be kept in mind by investigators of self-organization in biological systems, especially systems that are animal groups, lest we hold a falsely simplified view of life.

Acknowledgments

I am grateful to the National Science Foundation, National Geographic Society, and U.S. Department of Agriculture, whose financial support has made possible the bee research that underlies many of the ideas expressed in this essay.

Literature Cited

- Anderson, C., and J. J. Bartholdi, III. 2000. Centralized versus decentralized control in manufacturing: lessons from social insects. Pp. 92–105 in *Complexity and Complex Systems in Industry*, I. P. McCarthy and T. Rakotobe-Joel, eds. The University of Warwick, Warwick, UK.
- Anderson, C., and N. R. Franks. 2001. Teams in animal societies. *Behav. Ecol.* 12: 534–540.
- Anderson, C., and D. W. McShea. 2001. Individual versus social complexity, with particular reference to ant colonies. *Biol. Rev.* 76: 211–237.
- Bartholdi, J. J., III. 1993. Interactive program to balance assembly lines. *Int. J. Prod. Res.* 31: 2447–2461.
- Beebe, W. 1921. *Edge of the Jungle*. Henry Holt, New York.
- Bonabeau, E. 1998. Social insect colonies as complex adaptive systems. *Ecosystems* 1: 437–443.
- Bonabeau, E., G. Theraulaz, J.-L. Deneubourg, S. Aron, and S. Cam-

- azine. 1997. Self-organization in social insects. *Trends Ecol. Evol.* **12**: 188–193.
- Bonner, J. T. 1988. *The Evolution of Complexity*. Princeton University Press, Princeton.
- Bonner, J. T. 1998. The origins of multicellularity. *Integr. Biol.* **1**: 27–36.
- Bourke, A. F. G. 1999. Colony size, social complexity and reproductive conflict in social insects. *J. Evol. Biol.* **12**: 245–257.
- Camazine, S., J. Sneyd, M. J. Jenkins, and J. D. Murray. 1990. A mathematical model of self-organized pattern formation on the combs of honeybee colonies. *J. Theor. Biol.* **147**: 553–571.
- Camazine, S., J.-L. Deneubourg, N. R. Franks, J. Sneyd, G. Theraulaz, and E. Bonabeau. 2001. *Self-organization in Biological Systems*. Princeton University Press, Princeton, NJ.
- Crespi, B. J., and D. Yanega. 1995. The definition of eusociality. *Behav. Ecol. Sociobiol.* **6**: 109–115.
- Dawkins, R. 1982. *The Extended Phenotype: The Gene as the Unit of Selection*. Oxford University Press, Oxford.
- Drucker, P. F. 1988. The coming of the new organization. *Harvard Bus. Rev.* **66**: 45–53.
- Esch, H. 1967. The sounds produced by swarming honey bees. *Z. Vgl. Physiol.* **56**: 408–411.
- Goss, S., and J. L. Deneubourg. 1988. Autocatalysis as a source of synchronised rhythmical activity in social insects. *Insectes Soc.* **35**: 310–315.
- Hayek, F. A. von. 1945. The use of knowledge in society. *The American Economic Review* **35**: 519–530.
- Jeanne, R. L. 1986. The evolution of the organization of work in social insects. *Monit. Zool. Ital.* **20**: 119–133.
- Jenkins, M. J., J. Sneyd, S. Camazine, and J. D. Murray. 1992. On a simplified model for pattern formation in honey bee colonies. *J. Math. Biol.* **30**: 281–306.
- Karsai, I. 1999. Decentralized control of construction behavior in paper wasps: an overview of the stigmergy approach. *Artif. Life* **5**: 117–136.
- Keller, L. 1999. *Levels of Selection in Evolution*. Princeton University Press, Princeton.
- Lindauer, M. 1955. Schwarmbienen auf Wohnungssuche. *Z. Vgl. Physiol.* **37**: 263–324.
- Mackie, G. O. 1986. From aggregates to integrates: physiological aspects of modularity in colonial animals. *Philos. Trans. R. Soc. Lond. B.* **313**: 175–196.
- Maynard Smith, J., and E. Szathmáry. 1995. *The Major Transitions in Evolution*. Oxford University Press, Oxford.
- Michod, R. E. 1999. *Darwinian Dynamics: Evolutionary Transitions in Fitness and Individuality*. Princeton University Press, Princeton.
- Ratnieks, F. L. W., and C. Anderson. 1999. Task partitioning in insect societies. *Insectes Soc.* **46**: 95–108.
- Seeley, T. D. 1977. Measurement of nest cavity volume by the honey bee (*Apis mellifera*). *Behav. Ecol. Sociobiol.* **2**: 201–227.
- Seeley, T. D. 1995. *The Wisdom of the Hive: The Social Physiology of Honey Bee Colonies*. Harvard University Press, Cambridge, MA.
- Seeley, T. D. 1998. Thoughts on information and integration in honey bee colonies. *Apidologie* **29**: 67–80.
- Seeley, T. D., and S. C. Buhrman. 2001. Nest-site selection in honey bees: how well do swarms implement the “best-of-N” decision rule? *Behav. Ecol. Sociobiol.* **49**: 416–427.
- Seeley, T. D., and R. A. Morse. 1978. Nest site selection by the honey bee. *Insectes Soc.* **25**: 323–337.
- Seeley, T. D., and J. Tautz. 2001. Worker piping in honey bee swarms and its role in preparing for liftoff. *J. Comp. Physiol. A* **187**: 667–676.
- Shapiro, A. B., and C. D. Dworkin. 1998. *Bacteria as Multicellular Organisms*. Oxford University Press, Oxford.
- Simon, H. A. 1962. The architecture of complexity. *Proc. Am. Philos. Soc.* **106**: 467–482.
- Sober, E., and D. S. Wilson. 1998. *Unto Others: The Evolution and Psychology of Unselfish Behavior*. Harvard University Press, Cambridge.
- Strickland, T. R., C. M. N. Tofts, and N. R. Franks. 1992. A path choice algorithm for ants. *Naturwissenschaften* **79**: 567–572.
- Strickland, T. R., C. Tofts, and N. R. Franks. 1993. Algorithms for ant foraging. *Naturwissenschaften* **80**: 427–430.
- Theraulaz, G., and E. Bonabeau. 1995. Coordination in distributed building. *Science* **269**: 686–688.
- Theraulaz, G., E. Bonabeau, and J.-L. Deneubourg. 1998. The origin of nest complexity in social insects. *Complexity* **3**: 686–688.
- Weidenmüller, A., and T. D. Seeley. 1999. Imprecision in waggle dances of the honey bee (*Apis mellifera*) for nearby food sources: error or adaptation? *Behav. Ecol. Sociobiol.* **46**: 190–199.
- Wilson, E. O. 1971. *The Insect Societies*. Harvard University Press, Cambridge, MA.
- Wilson, J. 1999. *Biological Individuality*. Cambridge University Press, Cambridge, UK.